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Reverberating effects of resource exchanges in stream–riparian food webs

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Abstract

Fluxes of materials or organisms across ecological boundaries, often termed "resource subsidies," directly affect recipient food webs. Few studies have addressed how such direct responses in one ecosystem may, in turn, influence the fluxes of materials or organisms to other habitats or the potential for feedback relationships to occur among ecosystems. As part of a large-scale, multi-year experiment, we evaluated the hypothesis that the input of a marine-derived subsidy results in a complex array of resource exchanges (i.e., inputs, outputs, feedbacks) between stream and riparian ecosystems as responses disperse across ecological boundaries. Moreover, we evaluated how the physical properties of resource subsidies mediated complex responses by contrasting carcasses with a pelletized salmon treatment. We found that salmon carcasses altered stream–riparian food webs by directly subsidizing multiple aquatic and terrestrial organisms (e.g., benthic insect larvae, fishes, and terrestrial flies). Such responses further influenced food webs along indirect pathways, some of which spanned land and water (e.g., subsidized fishes reduced aquatic insect emergence, with consequences for spiders and bats). Subsidy-mediated feedbacks manifested when carcasses were removed to riparian habitats where they were colonized by carrion flies, some of which fell into the stream and acted as another prey subsidy for fishes. As the effects of salmon subsidies propagated through the stream–riparian food web, the sign of consumer responses was not always positive and appeared to be determined by the outcome of trophic interactions, such that localized trophic interactions within one ecosystem mediated the export of organisms to others.

Keywords Allochthonous resource · Donor control · Indirect effect · Pacific salmon · Tetragnathidae

Introduction

Ecosystems and their internal dynamics are affected by inputs, outputs, and feedback processes (Odum 1983; Meadows 2008). Many studies have examined how fluxes of materials or organisms from one habitat to another, often termed "resource subsidies," affect recipient food webs (Polis et al. 1997; Marczak et al. 2007; Allen and Wesner 2016), but few have addressed how such responses may, in turn, influence the fluxes of materials or organisms to other habitats or the potential for feedback relationships to occur among ecosystems. Because ecosystems are open to the exchange of materials in both directions, the input of a subsidy can quickly become an output if abiotic (e.g., gravity, wind, flowing water) or biotic (e.g., manipulation by scavengers) factors facilitate the continued movement of a resource through one ecosystem and into another. In addition, any ecological effects within an ecosystem may propagate across ecological

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boundaries to influence organisms in adjacent ecosystems (e.g., Baxter et al. 2004; Knight et al. 2005; Collins and Wahl 2017). Under such a scenario, the effects of one subsidy may determine those of another, a possibility that remains largely uninvestigated (but see Kraus and Vonesh 2012; Scharnweber et al. 2014; Collins and Wahl 2017). If a subsidy and its effects can disperse among multiple ecosystems, it is essential to understand how internal processes within an ecosystem (e.g., predation, grazing) mediate the output of resources to others. By studying the factor(s) that mediate such resource exchanges, ecologists may identify mechanisms which determine consumer responses and identify potential feedback effects that reverberate back and forth among ecosystems.

An evolving framework for understanding complex effects of resource subsidies may not only need to accommodate the potential for effects that reverberate among multiple habitats, but also address how properties of subsidies themselves influence potential for a resource and its effects to propagate through and feedback among ecosystems. Although resource subsidies are ubiquitous, their physical structure (i.e., how a subsidy is "packaged") and chemical composition (i.e., what constitutes a subsidy) vary dramatically, ranging from chemical compounds to the carcasses of whales. Differences in subsidy characteristics influence their pathways of entry into food webs and the efficiency at which they are processed or exploited (e.g., Cole et al. 2006; Hoekman et al. 2011). For instance, if predators disproportionately benefit from a certain subsidy (i.e., input), then their top-down effects on in situ organisms may be ameliorated or enhanced, thus mediating fluxes (i.e., output) of prey into other ecosystems (Newsome et al. 2015; Wesner 2016). In addition, subsidy properties could affect food-web responses by influencing how consumers perceive (e.g., sound, odor, erratic prey movements), are drawn towards (e.g., aggregating predators), or manipulate (e.g., scavengers redistributing carrion) a subsidy among habitats and ecosystems (Barton et al. 2013). These physical attributes are rarely distinguished, because in many studies, the subsidy itself is seldom the focus; rather, the consumer responses to the subsidy receive most attention. Yet, disentangling the influences of these subsidy characteristics may be a key to understand the complex array of direct, indirect and feedback effects of subsidies on food webs, especially when multiple resources are exchanged among ecosystems.

Stream–riparian ecosystems and resource subsidies associated with spawning migrations of Pacific salmon (*Oncorhynchus* spp.) provide an excellent context within which to investigate the potential for reverberating effects of subsidies among ecosystems, as well as the potential for subsidy characteristics to mediate such responses. Studies of multiple resource exchanges between aquatic and terrestrial ecosystems have a long history (e.g., Fisher and Likens 1972; Cummins 1974; Hynes 1975; Wallace et al. 1997; Baxter et al. 2005; Richardson et al. 2010), and spawning migrations of adult Pacific salmon (*Oncorhynchus* spp.) from marine to freshwater have been extensively studied as subsidies that alter the structure and function of aquatic and terrestrial communities of organisms (e.g., Gende et al. 2002; Janetski et al. 2009; Schindler and Smits 2017). Scavengers commonly transport salmon carcasses from streams to their adjacent riparian habitats, effectively subsidizing both ecosystems (e.g., Gende et al. 2002; Quinn et al. 2009). The post-spawning delivery of salmon carcasses to stream–riparian ecosystems is accompanied by a myriad of responses (e.g., Gende et al. 2002; Scheuerell et al. 2007; Quinn et al. 2009) yet most studies have focused on effects in a single recipient habitat (i.e., either freshwater or riparian) while acknowledging the potential for additional linkages between habitats. This gap represents an opportunity to explicitly investigate the potential for indirect and feedback effects of a subsidy across ecosystems.

As part of a large-scale, multi-year experiment, we investigated how the input of salmon carcasses (i.e., subsidy from marine ecosystem) to stream–riparian ecosystems affected resource outputs and the potential for feedbacks among ecosystems. We hypothesized that the input of a marine-derived subsidy results in a complex array of resource exchanges (i.e., inputs, outputs, feedbacks) between stream and riparian ecosystems as responses disperse across ecological boundaries. We assessed whether a subsidy (i.e., input) can create additional subsidies when effects disperse across ecological boundaries (i.e., output), and tracked organism responses through the food web to assess the potential for feedbacks between ecosystems. Furthermore, we assessed the degree to which trophic interactions mediate resource outputs and any indirect effects on animals subject to donor control in adjacent ecosystems. To test our hypothesis, we manipulated a repeated subsidy of salmon carcasses to stream–riparian ecosystems and allowed scavengers to remove carcasses from the stream. Responses of aquatic (larval and adult aquatic insects, fishes) and terrestrial (carrion flies, spiders, bats) organisms were compared to controls (no salmon carcasses added) as well as to a subsidy of pelletized salmon material with similar nutrient content but different physical structure. The salmon–pellet treatment acts as a type of control treatment that maintains some aquatic effects of the salmon carcass subsidy but removes the riparian effect, because terrestrial scavengers cannot remove the resource. By experimentally restricting the input of a subsidy to only stream ecosystems, we could disentangle effects between ecosystems. Salmon subsidies might increase both aquatic (e.g., larval and adult aquatic insects) and terrestrial (e.g., carrion flies) organisms, thus creating additional subsidies if these organisms disperse across ecological boundaries (e.g., emerging adult aquatic insects; inputs of terrestrial insects to streams), or not, depending on the extent to which community interactions mediate exchanges.

Materials and methods

Experimental design

We conducted a 3-year experiment in nine tributary drainages of the N. Fork Boise River, Idaho, USA, consisting of 500-m stream reaches treated with salmon carcasses ($n=3$), salmon carcass pellets ($n=3$), and untreated control reaches ($n=3$). Anadromous fishes including Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*O. mykiss*) were historically abundant in the Boise River and its tributaries (IDFG 1985; NWPCC 2004). However, the construction of multiple dams during the early 1900's eliminated salmon migrations into the Boise River for over a century. Streams were typical for the region (e.g., lithology, vegetation) and had similar resident fish assemblages (Redband trout *O. mykiss gairdneri*, Brook trout *Salvelinus fontinalis*, and Shorthead sculpin *Cottus confusus*). Carcass loading rates were based on a target of 0.5 salmon carcasses m^{-2} of wetted stream channel, chosen to reflect a high spawner density based upon historical data for streams of this region (IDFG 1985). Salmon–pellet treatment rates were adjusted to match phosphorus (P) application rates from salmon carcasses at 5.5 g P m^{-2}. Differences in N content of carcass and pellet subsidies resulted in an N application rate of 50 g N m^{-2} for carcass treatments and 27 g N m^{-2} for pellet treatments (Marcarelli et al. 2014; Collins et al. 2016). Carcass or pellet treatments were applied annually to the same 500-m reaches of their respective streams during the first week of August for 3 consecutive years (2008–2010).

Benthic insects

To investigate responses by benthic macroinvertebrates, these were sampled during July annually (2009–2010) at all nine streams. In each stream, seven riffle habitats were randomly sampled with a Surber sampler (0.09 m^2, 250 μm mesh size) to a depth of approximately 10 cm. Invertebrates were separated from detritus and lengths were measured to the nearest 0.5 mm. Biomass (dry mass) was calculated from taxon-specific length–weight relationships (Benke et al. 1999).

Consumption of insects by fish

To quantify the top-down effects of resident fishes on benthic insects, and to assess changes to terrestrial prey inputs, annual consumption of aquatic (benthic larvae, adults) and terrestrial insects by fishes was calculated using the trophic basis of production approach (Benke and Wallace 1980; Collins et al. 2016). Fish production (g m^{-2} $year^{-1}$) and gut content (proportion of dry mass) data were used to calculate the relative contribution of diet items to fish production (PF_{ij}), which was then used to estimate total annual consumption of diet items (Eq. 1; AC),

$$\mathrm{AC} = \frac{\mathrm{PF}_{ij}}{\mathrm{NPE} \times \mathrm{AE}_{ij}}, \tag{1}$$

where AEij represents the assimilation efficiency of food type i and NPE represents net production efficiency. We used the following AEs for resident trout and sculpin: 0.75 for benthic aquatic invertebrates and 0.70 for terrestrial invertebrates (Warren and Davis 1967; Elliott 1976). We set NPE as 0.21 and 0.12 for age 0 and age 1+, respectively, to account for allometric relationships between fish consumption and growth.

Aerial insects

To quantify relative biomass of aerial insects (including adult aquatic insects), a total of 1944 cylindrical sticky traps were deployed within riparian habitats at all 9 streams during 2009 and 2010. Traps (0.104 m^2) were coated in sticky resin and suspended from fence posts 1.3 m above the ground. Along six alternating transects per stream (75-m longitudinal spacing), sticky traps were placed at 0, 5, and 25 m perpendicular from the stream, for a total of 18 traps per stream. During the experiment, traps were deployed for approximately 14 days then replaced, ensuring continuous sampling over 12 weeks for each year (late June to mid-September). Aquatic and terrestrial insects were counted and identified to Order or Family, when possible. Subsets of individuals were measured to determine average length. Length–weight regressions were used to estimate biomass (dry mass) for each Order and Family (Sabo et al. 2002). Biomass of each Order was summed across all traps for each sample period, then averaged across all sample periods to determine the ambient levels of aerial insect biomass within riparian habitats.

Riparian predators

Two dominant families of orb-weaving spiders were observed within the riparian zone by nighttime visual surveys. Tetragnathidae (*Tetragnatha versicolor*; horizontal orb weavers) positions their webs parallel to the surface of water to capture emerging aquatic insects, whereas Araneidae (*Araneus* spp.; vertical orb weavers) captures both aquatic and terrestrial prey (Iwata 2007). Nighttime visual surveys were conducted annually (2009–2010) to quantify spider abundance within the stream reach. A total of 60 m of stream reach was surveyed per stream per sample period (July–August). Lateral surveys (0–5 m) indicated approximately 96% of Tetragnathidae and Araneidae abundance occurred within 1 m of the wetted edge, therefore, sampling was constrained to 1 m from the water's edge and vertically to 2.5 m on both sides of the stream. Riparian spiders were identified during surveys based upon spider morphological characteristics and web orientation (Ubick and Dupérré 2005).

Bat activity was acoustically monitored during spring, summer, and late summer with bat detectors (Anabat SD1) deployed at each of nine streams in locations chosen to reduce background noise (e.g., splashing water). Due to logistical constraints including limited quantities of recorders, three streams (Control–Banner; Analog–Pikes Fork; Carcass–Little Beaver) were sampled in 2009 and the remaining six (Control–Hungarian and Beaver; Analog–German and Hunter; Carcass–Big Owl and Trail) were sampled in 2010. Two detectors were deployed within study reaches for three night intervals at each stream. Bat insectivory was categorized based on generalized prey–habitat associations to detect how subsidy effects on aerial aquatic and terrestrial insects affected bat activity (Schnitzler et al. 2003). Bats foraging immediately above and near the surface of streams typically rely on aerial aquatic insects as prey, which we classified as stream-surface foragers (*Myotis yumanensis, M. californicus, M. lucifugus*; Ober and Hayes 2008). Bats foraging above the tops of riparian vegetation were classified as open-space foragers, and feed on aerial terrestrial and aquatic insects (*Myotis thysanodes, M. evotis, M. ciliolabrum, Eptesicus fuscus*; Ober and Hayes 2008). We expected foraging activity of both groups of bats would closely track changes in aquatic insect emergence and carrion fly abundance within riparian habitats. We reported bat activity as the average number of calls per night (three nights stream^{-1} season^{-1}), averaged across seasons (spring, May–June; summer, late July–August) to represent annual activity.

Statistical analyses

Analysis of variance with repeated measures (treatment and time were fixed factors) was used to evaluate the direct effects of salmon subsidies in different recipient habitats (i.e., stream vs. riparian), biomass of aquatic and terrestrial insects, the abundances of spiders, the activities of bats, and the annual consumption of prey by fishes. To differentiate magnitude of effects based on subsidy type, a priori contrasts of salmon carcass, salmon–pellets, and controls were conducted for all main effects ($\alpha = 0.05$). We distinguished responses by consumers as behavioral or demographic based upon knowledge of the organisms' life-history characteristics and behavioral traits.

General linear mixed effects models (GLMM) were used to examine the effect of treatments on the total relative biomass of adult aquatic insects and the abundance of riparian spiders while accounting for correlation among years within streams (SAS 9.4; Proc GLIMMIX; treatment as fixed factor; year as random factor; Gaussian distribution). Because predation by fishes on benthic insect larvae can affect emergence patterns of adult life stages (Baxter et al. 2004, 2005; Wesner 2016), and because resource subsidies can bolster predator populations and their top-down effects (Newsome et al. 2015), consumption of benthic insect larvae by stream fishes was included as a covariate to assess the mediating influence of predation intensity. By examining the interaction of treatment and predation intensity (i.e., consumption of benthic insect larvae), we examined whether subsidized fishes mediated patterns of adult aquatic insects by testing for the homogeneity of slopes (H_0: no difference between control and treatments). If subsidized fishes mediated patterns of adult aquatic insects, we predicted heterogeneity of slopes. The same approach was applied to evaluate whether fish predation and associated effects on aquatic insects also indirectly altered the abundance of riparian spiders that are subject to donor control of aquatic prey resources. Finally, we assessed the degree to which increased consumption of benthic insects by subsidized fishes positively or negatively correlated with the activities of bats in the surrounding riparian environment using correlation analysis ($r_{(d.f.)}$, p value). Given the inferential limitations of correlation analysis, any significant correlations suggest the potential for extended subsidy effects within a food web but should be cautiously interpreted with respect to causality.

The potential extended effects of subsidized terrestrial prey on terrestrial predators were also examined via correlation analysis ($r_{(d.f.)}$, p value). We explored whether the relative biomass of carrion flies within a streams riparian environment was correlated with the numbers of riparian spiders and the activities of bats. Additionally, because bats are predators of some spiders as well as insects, we examined correlations between bat-foraging activity and spider abundance. By assessing the correlations among subsidized prey and their predators, patterns could reveal potential indirect effects of subsidy additions in the terrestrial food web.

Results

Direct effects of subsidy additions

Direct effects of subsidies were detected on some food-web components, with the carcasses having consistently greater effects than the salmon–pellet. Standing stock biomass (mg dry mass m^{-2}) of benthic insects was two times higher in the carcass treatment (treatment, $F_{2,\,6} = 9.79$,

$p = 0.01$; carcass vs. control, $F_{1,\,6} = 18.46$, $p = 0.005$; Fig. 1a), whereas benthic insect responses to salmon–pellet addition were variable and did not differ from the carcass subsidy or control. The carcass-related increase in benthic insect biomass was eventually consumed by stream fishes. Annual consumption (g m^{-2} year^{-1}) of benthic insects by resident fishes tracked changes of these in-stream prey (treatment, $F_{2,\,6} = 6.28$, $p = 0.02$; Fig. 1b). In riparian habitats, translocated carcasses (presumably by black bears, *Ursus amaricanus*) increased the biomass of terrestrial carrion flies relative to controls (treatment, $F_{2,\,6} = 5.28$, $p = 0.04$; Fig. 1d). No direct effects of either salmon subsidy treatment were detected for the riparian spider families, Tetragnathidae (treatment, $F_{2,\,6} = 1.32$, $p = 0.36$; Fig. 1e) or Araneidae (treatment, $F_{2,\,6} = 1.04$, $p = 0.43$; Fig. 1e). Similarly, no direct effects of either salmon subsidy were detected for bat guilds that focus on aquatic (treatment, $F_{2,\,6} = 1.03$, $p = 0.41$) or terrestrial prey (treatment, $F_{2,\,6} = 0.68$, $p = 0.66$; Fig. 1f).

Feedbacks between ecosystems

By increasing the relative biomass of terrestrial carrion flies, salmon subsidy additions enhanced reciprocal feedbacks from riparian to stream habitats, as evidenced by the consumption of greater quantities of terrestrial invertebrates by stream fishes (Fig. 1c). Stream fishes consumed 4.5–4.8 times more adult carrion flies in carcass and pellet streams relative to controls (treatment, $F_{2,\,6} = 7.42$, $p = 0.01$). Because salmon carcasses, but not pellets, were removed and colonized by carrion flies, fly larvae (i.e., maggots) were consumed by stream fishes only in streams treated with salmon carcasses. Compared to control streams, consumption of adult aquatic insects by fishes was approximately 4 and 15 times greater in streams treated with salmon–pellet and carcasses, respectively (treatment, $F_{2,\,6} = 6.23$, $p = 0.02$). In total, consumption of terrestrial prey (i.e., subsidy-mediated feedback) by fishes was 2.6 times greater in streams treated with carcasses versus salmon–pellets.

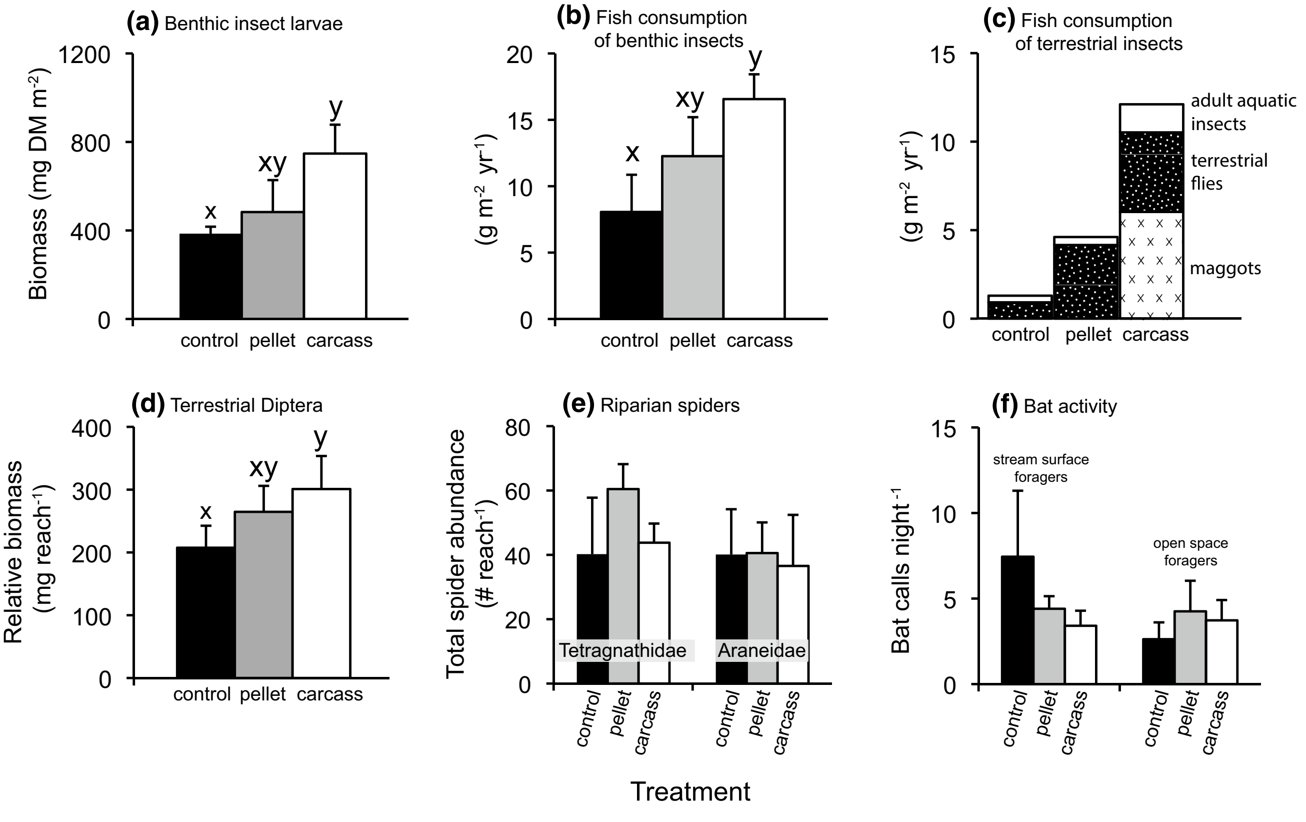

Fig. 1 Comparison of main food-web responses ($n = 3$; average ± SE) between a salmon subsidy that remains within a stream (pellet) and salmon carcasses which are naturally distributed among aquatic (**a**, **b**) and riparian (**c**, **e**) habitats: **a** standing stock biomass (dry mass) of benthic insect larvae; **b** annual consumption of benthic insect larvae by resident fishes; **c** annual consumption of terrestrial insects: note description beside each pattern; **d** average relative biomass (dry mass) of carrion flies within the riparian habitats of study streams; **e** average total abundance of Tetragnathidae and Araneidae in riparian habitats; and **f** annual activity of bats based on guilds foraging near edges of vegetation and above the surface of streams and bats foraging in the open canopy (open space). Letters above columns denote significant treatment differences

Mediation of cross-boundary subsidy effects

Fish predation pressure on aquatic insect larvae (see above) mediated emergence patterns of adult life stages differently among control and treatments (GLMM: consumption × treatment, $F_{2,6} = 13.5$, $p = 0.006$; Fig. 2a). In control streams, the relative biomass of adult aquatic insects positively tracked fish predation ($\beta = 36.2$, SE = 6.3, $p = 0.001$). In carcass treatments, greater consumption of benthic larvae corresponded with a decrease in adult aquatic insect biomass in the riparian zone (GLMM: consumption × carcass, $\beta = -40.37$, SE = 7.9, $p = 0.002$; Fig. 2a). Because pellet effects were not as pronounced as carcasses, such a pattern was not observed for pellet treatments (GLMM: consumption × pellet, $\beta = 16.4$, SE = 9.8, $p = 0.09$). In subsidized streams where biomass of larval insects increased (Fig. 1a), extrapolations from pellet and carcass models predict greater biomass of adult aquatic insects in the riparian zone at low fish predation levels (0–5 g m^{-2} $year^{-1}$; Fig. 2a). However, as fish production increased from many food-web sources (aquatic and terrestrial prey; Fig. 1b, c), predation intensified (i.e., fish eat more larval insects) and fewer aquatic insects were present in the riparian zone.

Indirect effects of subsidies on riparian predators

By mediating resource exchanges from stream to riparian ecosystems, subsidized fishes indirectly influenced some terrestrial predators through shared prey resources (i.e., a donor-control mechanism). For instance, in streams where subsidized fishes consumed more benthic larvae and reduced the biomass of adult aquatic insects, there were fewer Tetragnathidae spiders in carcass (GLMM: consumption × carcass, $\beta = -7.1$, SE = 3.1, $p = 0.06$; Fig. 2b) and pellet (GLMM: consumption × pellet, $\beta = -7.9$, SE = 3.7, $p = 0.08$; Fig. 2b) treatments than would be expected based on patterns observed in control streams, although models were not significant at an alpha of 0.05. In contrast, Araneidae spiders exhibited no response to either treatment (GLMM: consumption × treatment, $F_{2,6} = 0.13$, $p = 0.87$). Additionally, streams with the highest consumption of benthic insects (Fig. 1b) were inversely correlated with the foraging activities of stream-surface bats ($r_{(9)} = -0.73$, $p = 0.02$; Fig. 3a), whereas open canopy foragers exhibited no pattern ($r_{(9)} = -0.39$, $p = 0.29$).

By directly increasing the relative biomass of terrestrial carrion flies in riparian ecosystems (Fig. 1d), salmon subsidy additions appeared to indirectly influence select riparian predators based on a series of prey–predator correlations (Table 1). For instance, riparian environments with a higher relative biomass of carrion flies had fewer Araneidae spiders ($r_{(9)} = -0.77$, $p = 0.01$; Fig. 3b, white circles) and higher activities of open-canopy foraging bats ($r_{(9)} = 0.75$, $p = 0.02$; Fig. 3b, black circles). Additionally, sites with higher activities of open-canopy foragers were associated with fewer Araneidae spiders ($r_{(9)} = -0.85$, $p = < 0.01$; Fig. 3c).

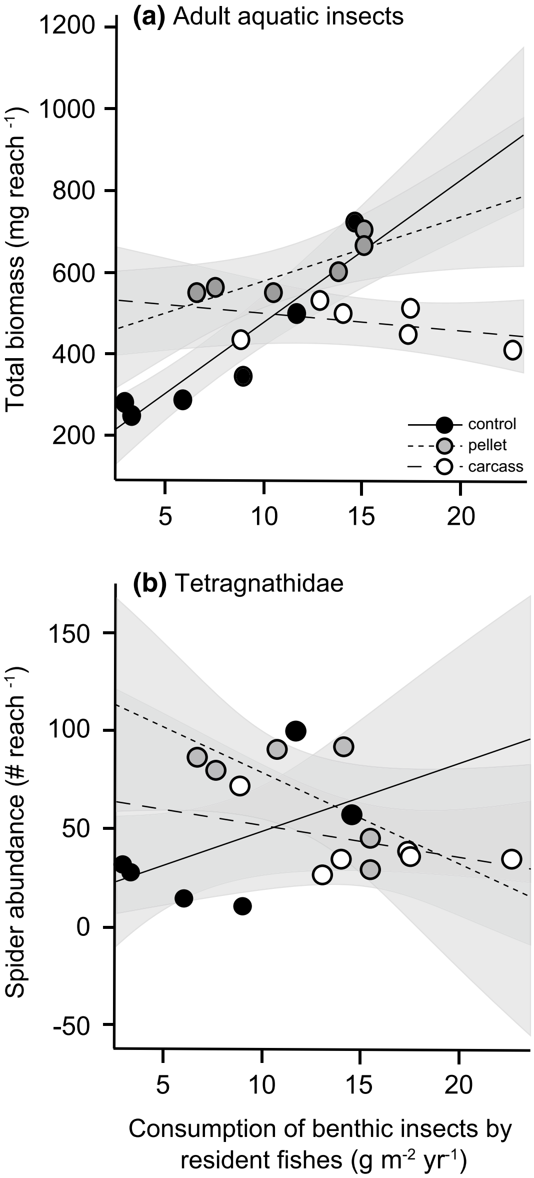

Fig. 2 **a** Direct effects of subsidized fishes and their consumption of benthic insect larvae (i.e., predation pressure) on the mean relative biomass (dry mass) of adult aquatic insects sampled on sticky traps within riparian habitats. **b** Indirect effect of subsidized fishes on the abundance of Tetragnathidae spiders, a riparian predator that rely on aquatic prey and are subject to donor control. In each panel, linear models and associated 95% confidence intervals (shaded bands) were estimated for salmon carcass (long dash), salmon–pellet (short dash), and control (solid line) treatments. Overlaid circles represent raw data values from 2009 to 2010. Black circles = control ($n = 6$), gray circles = pellet subsidy ($n = 6$), white circles = carcass subsidy ($n = 6$)

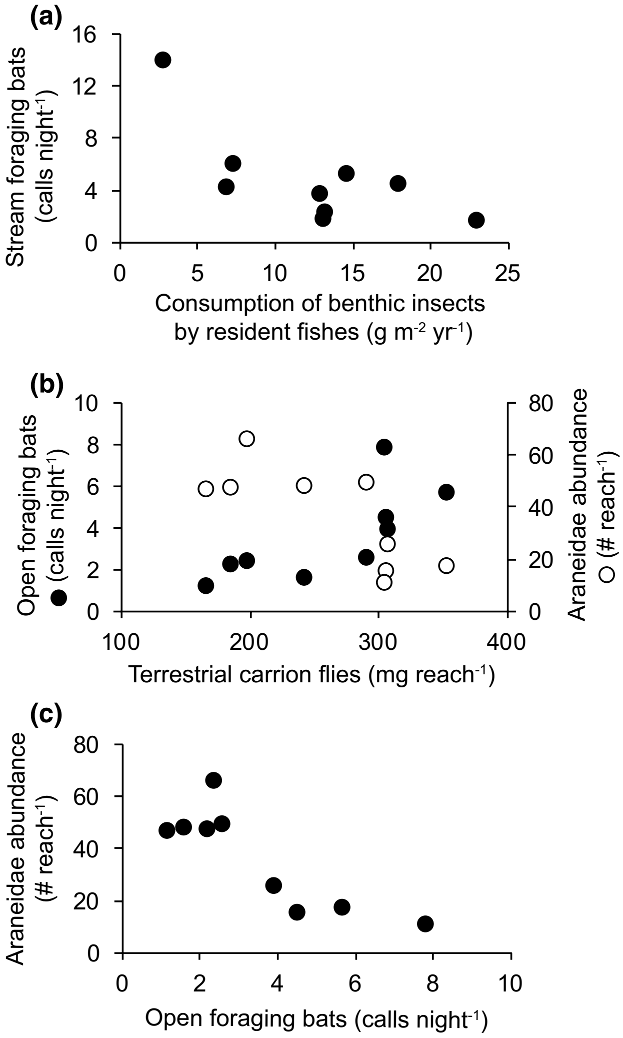

Fig. 3 **a** Pairwise comparison of subsidized stream fishes and their consumption of benthic insect larvae with the foraging activity of stream-surface foraging bats (*Myotis yumanensis, M. californicus, M. lucifugus*) to assess the potential for donor control between subsidized fish and a riparian predator. **b** Pairwise comparisons of subsidized terrestrial carrion flies with Araneidae spiders (white circles) and open-space foraging bats (*Myotis thysanodes, M. evotis, M. ciliolabrum, Eptesicus fuscus*; black circles). **c** Pairwise comparison of predatory Araneidae spiders and open-space foraging bats to assess the potential for intra-guild predation. $N = 9$ in all panels. See Table 1 for p values and correlation coefficients

Discussion

A suite of behavioral and numeric organismal responses that propagated across the land–water boundary shaped the subsidized stream–riparian food web in our large field experiment. Consequently, ecosystems were both recipients (i.e., receiving resource inputs) and donors (e.g., resource outputs) of resource exchanges (Fig. 4). Consistent with our hypothesis, inputs of salmon carcasses altered stream–riparian food webs by directly subsidizing multiple aquatic and terrestrial organisms (e.g., benthic insect larvae, fishes, and terrestrial carrion flies; Fig. 4a, b). Such responses further influenced food webs via indirect effects along pathways within an ecosystem as well as across land and water (e.g., subsidized fishes altered aquatic insect emergence and, in turn, the abundance and activity of select spiders and bats; Fig. 4b–d). As effects of salmon subsidies propagated through the stream–riparian food web, the sign of consumer responses was not always positive and appeared to be determined by the outcome of trophic interactions, such that localized trophic interactions within one ecosystem mediated the output of organisms to another ecosystem (e.g., Figure 4d). Finally, by contrasting salmon carcass and pellet subsidies, we demonstrated that physical properties of a subsidy (i.e., how it is "packaged") influenced the origin of responses, the magnitude of its effects, and the emergence of feedback pathways (Fig. 4c).

We detected a feedback pathway that occurred as resources were recycled between land and water (Kraus and Vonesh 2012; Scharnweber et al. 2014). Terrestrial scavengers, primarily black bears (S.F. Collins, personal observations), facilitated (or mediated) the transfer of salmon carcasses to the riparian zone (20–31 carcasses per 100 m, as estimated in 2010; Collins and Baxter 2014) which had important consequences for food-web responses that did not accompany the salmon–pellet treatment. The simple act of moving (i.e., as an output from the stream) carcasses to riparian areas increased carrion fly larvae and adults, many of which fell into streams and were consumed by fishes (Fig. 4c), and which contributed to enhanced fish growth rates (Collins et al. 2016). This feedback was relatively short lived, as carcasses were quickly consumed by carrion larvae

Table 1 Exploratory pairwise comparisons of subsidized terrestrial carrion flies (Diptera) (1) and riparian predators (2–5) to assess the potential for indirect effects resulting from experimental salmon subsidy additions

Variable	1	2	3	4	5
(1) Terrestrial carrion fly biomass		*0.33*	***0.01***	*0.06*	***0.02***
(2) Tetragnathidae spiders	0.37		*0.83*	*0.33*	*0.45*
(3) Araneidae spiders	**−0.77**	−0.09		*0.28*	***<0.01***
(4) Stream-surface foraging bats	−0.64	−0.37	0.40		*0.34*
(5) Open-space foraging bats	**0.75**	0.29	**−0.85**	−0.36	

The correlation matrix reports p values (italicized) and correlation coefficients (unitalicized). Bold values indicate statistical significance at $\alpha = 0.05$. $N = 9$ for all pairwise comparisons

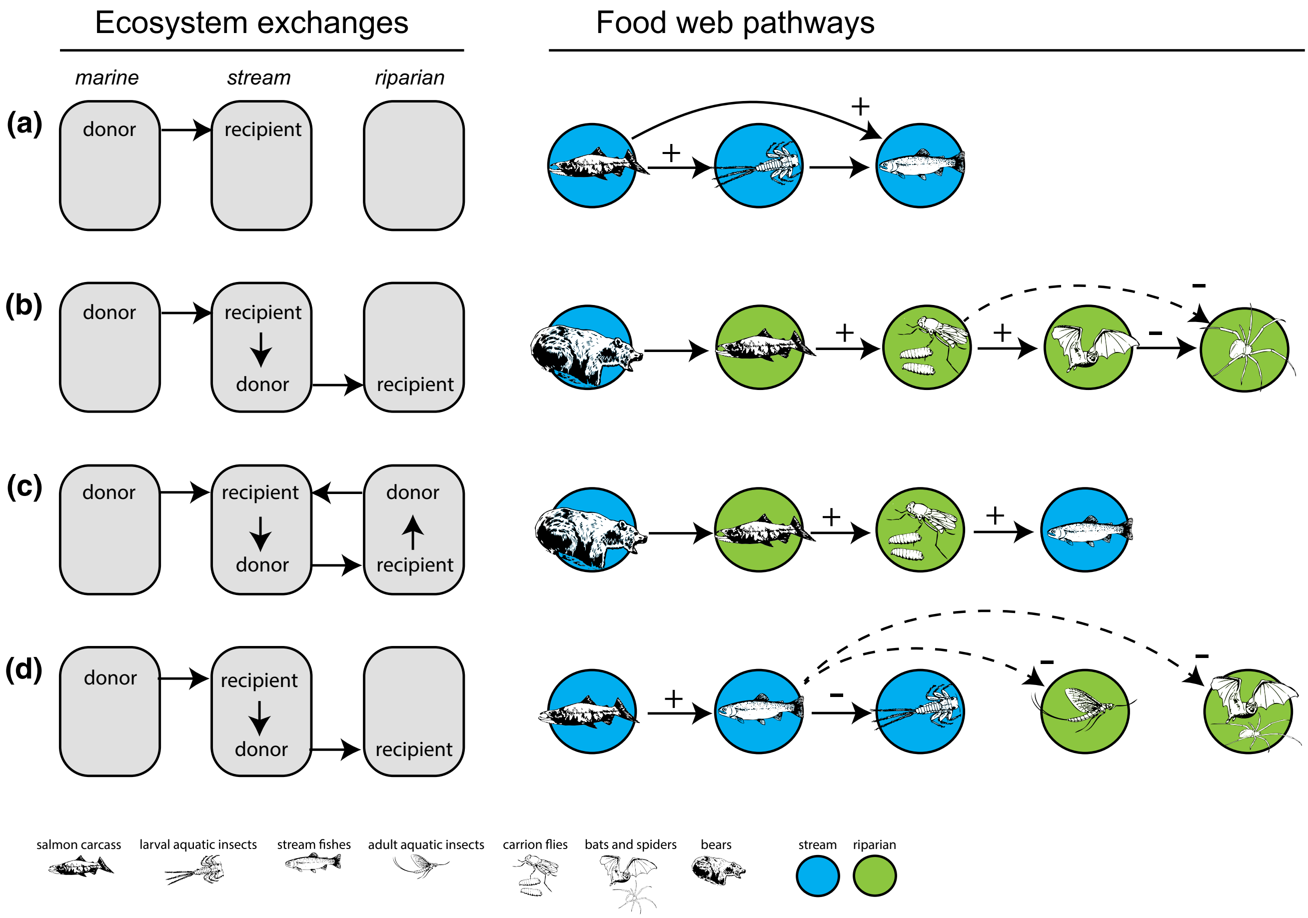

Fig. 4 General summary of the complex direct, indirect, and feedback effects observed in stream–riparian ecosystems receiving experimental additions of Pacific salmon carcasses. Each level indicates: (left) the generalized exchange (inputs and outputs) of resources among ecosystems and (right) the aquatic and terrestrial organisms responsible for driving the observed patterns. Circle color represents the location of responses (blue = stream; green = riparian) as they propagate between land and water. Solid lines signify direct effects. Dashed lines signify indirect effects. Symbols signify the sign of ecological effect (color figure online)

(Collins and Baxter 2014). Yet, in this short time, terrestrially assimilated carbon was returned to the stream ecosystem where fishes benefitted. This array of findings paints a more complex picture of the effects of resource subsidies on food webs than is typically depicted when effects are evaluated in a single, recipient ecosystem.

Within stream and riparian ecosystems, we detected strong direct responses to salmon subsidies, which were accompanied by indirect effects on in situ prey through mechanisms akin to apparent competition (Holt 1977; Murakami and Nakano 2002; Sabo and Power 2002). For instance, resident trout were subsidized through multiple food-web pathways, which fueled their productivity (see Collins et al. 2016) and predation pressure on benthic invertebrates (inferred via the annual consumption of benthic insect larvae) throughout the year. A similar pattern was observed among terrestrial organisms based on a suite of correlations among carrion flies, Araneidae spiders, and bats. Although salmon subsidies directly increased carrion flies, we detected a negative correlation with Araneidae spiders (generalist predators), such that more carrion flies corresponded with fewer Araneid spiders. Additionally, the activity of open-canopy foraging bats (e.g., comprised of *Myotis thysanodes, M. evotis, M. ciliolabrum, Eptesicus fuscus*; Ober and Hayes 2008) positively tracked the relative biomass of carrion flies. These bats frequently glean prey like spiders from vegetation (Schnitzler et al. 2003) and were negatively correlated with Araneidae spiders. Such correlations suggest the potential for apparent competition between subsidized carrion flies and Araneid spiders via a shared predatory guild of bats. These potential subsidy-mediated indirect effects deserve more focused investigation, as the sign and magnitude of such indirect interactions are important to theory-based expectations regarding the role of resource subsidies in communities (e.g., Polis et al. 1997; Holt 2004; Takimoto et al. 2009) and have been the subject of contrasting empirical findings (e.g., Nakano et al. 1999; Henschel et al. 2001; Murakami and Nakano 2002; Spiller et al. 2010). The analytical framework we applied here does not provide mechanistic certainty regarding these relationships. On the other hand, the duration of our experiment allowed both behavioral and numerical responses to play out over multiple years, which may explain our observation of negative indirect effects of subsidies on in situ prey rather than the positive effects sometimes observed during short-term experiments.

Our observations also demonstrate that indirect subsidy effects propagated across ecological boundaries to influence organisms in adjacent habitats through donor control. We expected effects of salmon subsidies might propagate into riparian habitats through increased emergence of aquatic insects and benefit riparian predators (e.g., Baxter et al. 2005). We found the opposite, as subsidized fishes and their predatory effects on larval benthic insects mediated patterns of emergence of adult life stages; a pattern that may be widespread (see Wesner 2016). By mediating emergence, enhanced predation by subsidized fishes indirectly reduced the abundance of Tetragnathid spiders, which exhibit preference for small-bodied insects like midges (Williams et al. 1995). Likewise, we found strong negative correlations between fish consumption of benthic insects and the activity of surface trawling bats that tend to feed on adult aquatic insects (e.g., *Myotis yumanensis, M. californicus, M. lucifugus*; Ober and Hayes 2008). Our results suggest the possibility that alterations to fish productivity can indirectly influence the numbers and activities of certain terrestrial organisms that share common prey and are subject to donor control.

Our results suggest that biophysical properties, or the physical forms, of subsidies are an important dimension of what constitutes the "quality" of such resources, because they influence how organisms perceive and interact with a subsidy. Characteristics like lipid or nutrient content are undoubtedly important (Marczak et al. 2007; Marcarelli et al. 2011; Bartels et al. 2012), but organisms such as predators, scavengers, and saprophages may not perceive such properties directly. Instead, many consumer–subsidy interactions are facilitated by scents, sounds, and movements. The most apparent distinction we detected between the two salmon subsidies was the facilitated transfer of carcasses from streams to the wetted margins of streams and into riparian habitats. Although not visually striking, the release of odiferous chemical compounds through the decomposition of salmon materials also appeared to attract a range of organisms. By attracting carrion flies and scavengers, the physical and chemical characteristics of carcasses were responsible for a series of food-web responses that drove energy recycling between ecosystems. As the study of resource subsidies embraces more of the natural complexity associated with these phenomena, consideration of subsidy properties may provide a straightforward means of tying the characteristics of subsidies to the traits of consumers that use them. Moreover, as studies begin to examine concurrent resource exchanges between ecosystems, variation in the biophysical properties should aid in understanding food-web responses.

The responses we observed to the experimental addition of whole salmon carcasses and artificial salmon–pellets were linked to the specific properties of these subsidies and their attendant interactions with organisms, raising implications not only for the fundamental ecology of resource subsidies but also for managing salmon and their ecosystems. Although suites of effects were observed, these artificial subsidy additions likely differ from natural spawning events in other ways. Artificial additions of salmon carcasses are not accompanied by the influences of live salmon, such as excretion of nutrients, spawning disturbance of streambeds, and deposition of eggs, all of which are important aspects of the role of salmon in freshwater ecosystems (e.g., Scheuerell et al. 2007; Tiegs et al. 2009; Collins et al. 2011). Though such differences between an inanimate mitigation tool and live spawning salmon may appear self-evident, from a policy perspective, this distinction has not been drawn, because the focus has been on nutrient content, not consumer–subsidy interactions (reviewed in Collins et al. 2015). Well-intentioned efforts to mitigate for the loss of Pacific salmon may be less successful, because fish and wildlife will be affected differently depending on the form of the resource used. Wildlife were also affected by the loss of Pacific salmon migrations, and as our experiment demonstrated, play an important role in mediating food-web responses. Nevertheless, salmon carcasses, pellets, and inorganic fertilizers are being used with increased frequency as a means of mitigation on the basis that the nutrients themselves are of principal importance. We suggest otherwise based on the results of this experiment.

Although many studies examine the effects of resource subsidies on a single, recipient ecosystem, such a unidirectional perspective on the flow of materials from one ecosystem to another may promote an overly simplistic view of complex exchanges of materials. In contrast to this binary framework, landscapes are a complex and heterogeneous configuration of habitats and ecosystems whose linkages are likely to be equally complex (e.g., Turner et al. 2001). In such landscapes, movements of organisms play an important role in structuring extended food webs, as emphasized by numerous theoretical and model-based studies (McCann et al. 1998; Holt 2002; Rooney et al. 2008), as well as the emerging "meta-community" (Leibold et al. 2004) and "meta-ecosystem" (Loreau et al. 2003) frameworks. Indeed, the results of our experiment suggest that a spatial ecology of food webs and resource subsidies would be better served by linking to these frameworks and empirically confronting their associated models (as recently called for by Gounand et al. 2018) than by further attempts to adapt the classic donor–recipient model to the complexity of food webs in landscapes.

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Author contribution statement MSW, GS, CVB, AMM, LF planned and designed the experiment. SFC, AMM, and CVB collected stream food web and spider data. SF and LF collected bat data, and SFC analyzed the data. SFC wrote the first draft of the manuscript, and all authors contributed to revisions.

Compliance with ethical standards

Ethical approval All applicable institutional and/or national guidelines for the care and use of animals were followed.

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